

ON THE IDENTITY OF THE AMPHIBIAN *HESPEROHERPETON GARNETTENSE* FROM THE UPPER PENNSYLVANIAN OF KANSAS

by ANDREW R. MILNER

ABSTRACT. *Hesperoherpeton garnettense* Peabody was first described as an embolomereous anthracosaurian amphibian, based on a small scapulocoracoid and associated neural arch from the Upper Pennsylvanian of Garnett, Kansas. Subsequently, on the basis of a referred specimen from the type locality, *Hesperoherpeton* was claimed by Eaton and Stewart to be the most anatomically primitive tetrapod despite its Upper Pennsylvanian age. Re-examination of the type and the referred specimen leads to the conclusion that the former is indeterminate and the latter is a poorly preserved small specimen of a temnospondyl amphibian of the family Trematopidae. It may be a specimen of the trematopid *Actiobates peabodyi* Eaton from the same locality. The binomen *H. garnettense* is a *nomen dubium* restricted to the type specimen, and Eaton and Stewart's Order Plesiospoda is invalid.

THE Upper Pennsylvanian tetrapod assemblage from Garnett in eastern Kansas is unique among Carboniferous faunas in that it is made up largely of diapsid and pelycosaurian reptiles (Reisz 1981; Reisz *et al.* 1982). Only three amphibian specimens from Garnett have been described. One of these, *Actiobates peabodyi* Eaton 1973 is a temnospondyl of the family Trematopidae (Milner: in prep.). The other two specimens form the subject of this study. In 1958, Peabody described a small scapulocoracoid and associated neural arch from Garnett as the new taxon *Hesperoherpeton garnettense* which he assigned to the family Cricotidae within the embolomereous anthracosaurs. In 1960, Eaton and Stewart described a second specimen from Garnett which they attributed to *Hesperoherpeton*. This specimen comprised the crushed and disarticulated anterior skeleton of a small amphibian, which Eaton and Stewart reconstructed, concluding that it was not an embolomere but was quite unlike any other known fossil amphibian. Despite its late Pennsylvanian age, Eaton and Stewart interpreted *Hesperoherpeton* as the most primitive known tetrapod, a relictual form structurally intermediate between rhipidistian fishes and tetrapods and they made it the basis of a new order Plesiospoda. This order was erected as a grade group characterized by a mixture of choanate fish characters (large notochordal canal, divided braincase, postaxial processes on some fore-limb elements, and probable articulation between tabular and pectoral girdle) and tetrapod characters (tetrapod pectoral girdle, digits, otic notch, nostrils separate from jaw margin and rhachitomous vertebrae). Eaton and Stewart also placed *Hesperoherpeton* in the monogeneric family Hesperoherpetonidae defined by its unique specializations, notably the squamosal bordering the orbit and the loss of most of the circumorbital series. As the skull is both disarticulated and incomplete, it is difficult to understand how such unique characters were identified. The presence of postaxial processes on some limb bones neatly fulfilled a prediction about primitive tetrapod limb structure made by Eaton several years previously (Eaton 1951) and elaborated subsequently (Eaton 1960). Most later workers on Palaeozoic tetrapods who have examined this material or discussed tetrapod origins, have either treated Eaton and Stewart's interpretation with extreme caution (Romer 1968, p. 88; Olson 1971, p. 292) or have ignored it altogether (Thomson and Bossy 1970; Carroll and Winer 1977; Rosen *et al.* 1981; Reisz *et al.* 1982). The only alternative systematic position suggested for it was a doubtful placement within the Seymouriamorpha by Romer (1966, p. 363) followed by Kuhn (1972, p. 43). However, in some more general accounts of amphibian evolution it has been cited as a very primitive tetrapod illustrating an intermediate condition between fishes and

tetrapods (Schmalhausen 1968, pp. 54, 62; Porter 1972, p. 93, Vorob'yeva 1974, p. 222; Alexander 1975, p. 235).

During 1979 I was able to examine the two *Hesperoherpeton* specimens and make a number of observations which suggest a more mundane interpretation of this material. Although precise systematic placement of the two specimens is not possible, this reinterpretation does provide a refutation of the status given to them by Eaton and Stewart.

MATERIAL

KUVP 9976 The holotype of *H. garnettense* Peabody 1958. Collected in 1954 and figured by Peabody (1958, text-fig. 1), Eaton and Stewart (1960, fig. 8), and in this work (text-fig. 1A, B).

KUVP 10295 Referred specimen of Eaton and Stewart 1960. Collected in 1955 and figured by Eaton and Stewart (1960, fig. 1-7 and 9-11) and in this work (text-figs. 2B-4).

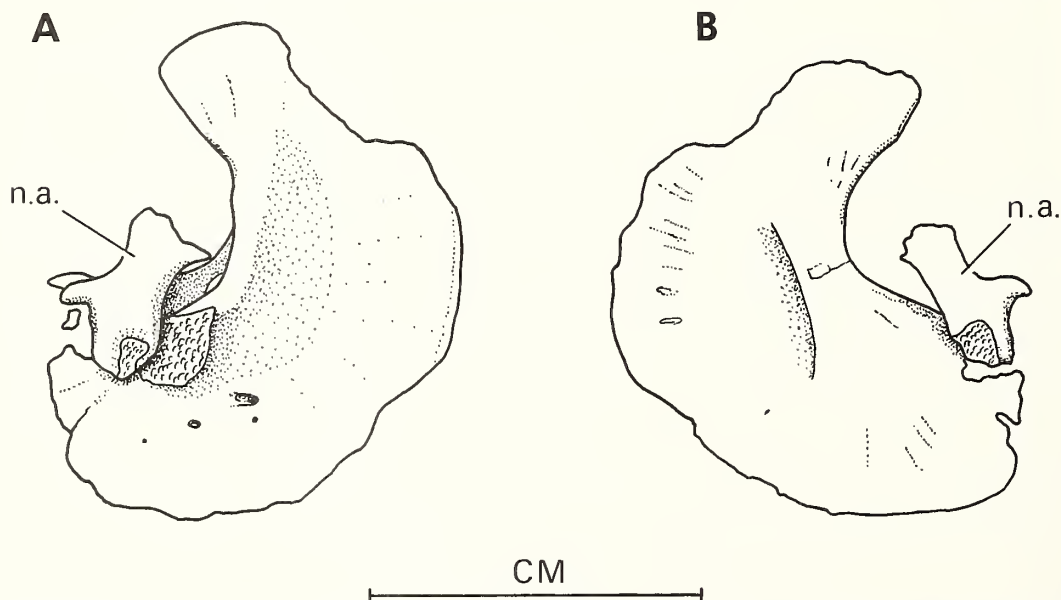
Both specimens are housed in the Vertebrate Paleontology collections (KUVP) of the Museum of Natural History at the University of Kansas, Lawrence, Kansas.

Locality and Horizon. Quarry 10 km north-west of Garnett, Putnam Township, Anderson County, Kansas. Rock Lake Member, Stanton Formation, Lansing Group, Missourian Series, Upper Pennsylvanian. Reisz *et al.* (1982) provide further information on the locality and the detailed local stratigraphy.

DESCRIPTIONS

The holotype specimen

KUVP 9976 consists of a small right scapulocoracoid and a neural arch in close association. The originally exposed surface has been embedded in plastic and the specimen subsequently prepared out



TEXT-FIG. 1. A, B, *Hesperoherpeton garnettense* Peabody (*nomen dubium*). KUVP 9976, the holotype and only specimen from Garnett, Kansas. Right scapulocoracoid in A, external aspect, B, internal aspect, together with associated neural arch. n.a.—neural arch.

so that the two bones are visible from both sides. The specimen was figured by Peabody (1958, text-fig. 1) and, less accurately, by Eaton and Stewart (1960, fig. 8) but is refigured here for ease of reference (text-fig. 1A, B) although the figure, drawn directly from the specimen, contains no new information.

The neural arch is not co-ossified to a centrum and has a low neural spine. The former feature indicates that it cannot be attributed to the orders Nectridea, Aistopoda, Microsauria, or any amniote group. The absence of swollen neural arches suggests, albeit from negative evidence, that it is not a seymouriamorph. Peabody suggested that it belonged to an embolomerous form as the symmetrical anterior and posterior faces of the pedicels implied the presence of equally large intercentra and pleurocentra. However, although the pedicel faces are asymmetrical in some rhachitinous forms, they are symmetrical or nearly so in others (*Neldasaurus* Chase 1965, fig. 9A; *Eryops* Moulton 1974; *Tersomius* Daly 1973, text-figs. 5A and 6). Thus the neural arch does not characterize the specimen as an embolomerous anthracosaur but simply as either a temnospondyl or an anthracosaur or a more primitive stem-tetrapod.

The scapulocoracoid is well ossified for its size and this suggests that it belonged to a terrestrial form, small aquatic amphibians having unossified or poorly ossified endochondral regions in the pectoral girdle. The shape of the scapulocoracoid resembles that of labyrinthodont-grade amphibians rather than of reptiles. The presence of supracoracoid and glenoid foramina below the glenoid resembles the condition in both temnospondyls (*Greererpeton* Holmes 1980, *Dissorophus* DeMar 1968) and anthracosaurs (*Proterogyrinus* Holmes 1980). The glenoid is large and slightly triangular as originally described by Peabody, not a small ovoid as interpreted by Eaton and Stewart, and it resembles that in terrestrial temnospondyls such as *Trematops* (Olson 1941, fig. 11B).

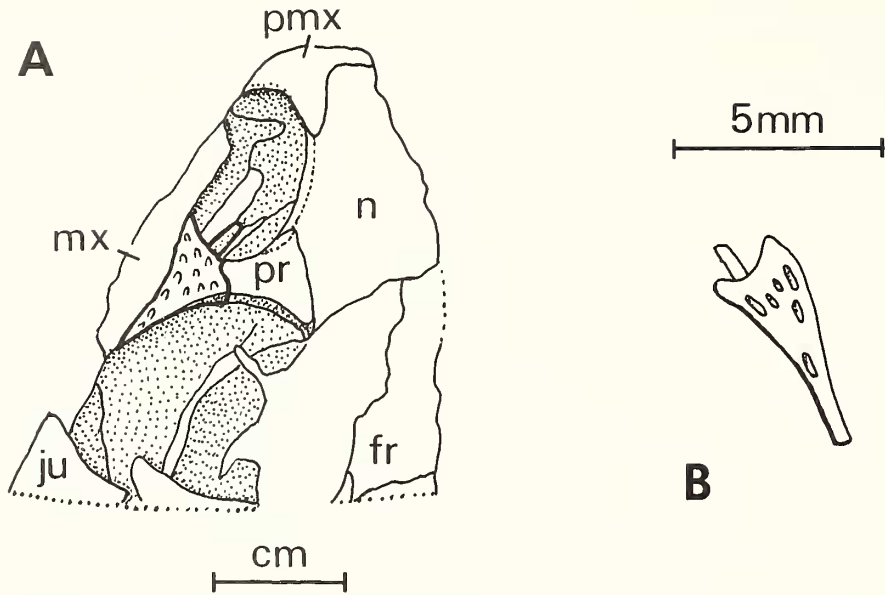
In conclusion, the holotype specimen of *H. garnettense* appears to be an indeterminate labyrinthodont-grade amphibian, possibly a terrestrial temnospondyl. The bones are entirely consistent with attribution to a trematopid temnospondyl such as *Actiobates* which occurs at Garnett, but are equally consistent with attribution to a small member of the Dissorophidae or Eryopidae. Thus the binomen *H. garnettense* is a *nomen dubium* restricted to an indeterminate holotype specimen.

The referred specimen

KUVP 10295 consists of a large number of small bones on a small slab of shale. The originally exposed surface has been embedded in plastic and the specimen has been prepared from the back. As noted by Eaton and Stewart (1960, p. 220) the bones are mostly broken or distorted by crushing and are also scattered. All the identifiable bones are consistent in size, number, and general relative position with the interpretation that they derive from the anterior half of a single, small amphibian skeleton. The anterior appendicular skeleton and the anterior trunk are most readily recognized, being only slightly disarticulated, the posterior skeleton is absent, whilst the skull is severely crushed and scattered. Regrettably, some elements are now difficult to observe through the plastic coat. However, I have been able to identify and draw several bones which I believe are sufficient to permit a reassessment of this specimen. These include some elements of the skull roof, palate, mandible, axial and anterior appendicular skeleton. Unfortunately I was unable to identify the braincase, stapes, or occiput amongst the crushed cranial elements at one end of the slab: those skull bones which are figured and described here being a group which have drifted back towards the pectoral region. Some of the identified bones are figured in text-figs. 2B-4 and are described in the following paragraphs.

Skull. Five cranial elements have been confidently identified, namely a right lachrymal, a left postfrontal, a right squamosal, a right vomer, and a left pterygoid.

The right lachrymal (text-figs. 2B and 3) is the most diagnostic element in the specimen. It is present as a disarticulated bone and was described and figured by Eaton and Stewart (1960, fig. 3C, D) as the right tabular. It consists of an elongate triangular plate of lightly sculptured dermal bone with a long slender process extending ventrolaterally from the unsculptured surface along its long axis (text-fig. 2B). Eaton and Stewart interpreted this as a tabular with a small otic notch supported by a flange of the



TEXT-FIG. 2. A, *Actiobates peabodyi* Eaton. KUVV 17941, the holotype specimen. Left anterior region of the skull based on Eaton 1973, fig. 1a and on first-hand observation of the specimen. The lachrymal is heavily outlined and sculpture pits are depicted on it. Abbreviations are: fr—frontal, ju—jugal, mx—maxillary, n—nasal, pmx—premaxillary, pr—prefrontal. B, indeterminate trematopid. KUVV 10295, isolated ossification interpreted as right tabular by Eaton and Stewart, but here identified as the right lachrymal of a trematopid.

dermal surface and by the slender process. In their discussion they suggested that the slender process may have articulated with the pectoral girdle in a rhipidistian-like manner. There is no precedent for a tabular of this particular shape in the lower tetrapods and as the bone occurs as an isolated structure, its identification as a tabular would appear to have been no more than a guess. However, its precise shape and size relative to the other bones are entirely consistent with it being a lachrymal of a temnospondyl amphibian of the Family Trematopidae. The Trematopidae are a family of dissorophoid amphibians characterized by several features, most conspicuously the elongate external naris (Olson 1941; Bolt 1974a). Within the Order Temnospondyli, this type of external naris, with a posterior extension and a characteristic configuration of surrounding bones is unique to the Trematopidae, although a similar arrangement occurs in the Upper Permian batrachosaur *Chroniosaurus* from Russia (Tverdochlebova 1972). Such a narial structure has been claimed for the dissorophid *Longiscitula houghae* (DeMar 1966; Boy 1981) but Bolt (1974a) notes that this is doubtful and I can confirm, having examined this specimen, that the 'elongate nostril' is an artifact of crushing. In the trematopids the posterior extension of the naris is a manifestation of modifications to the nasal, prefrontal, lachrymal, maxillary, and vomer (Bolt 1974a). The primitive temnospondyl lachrymal condition is a roughly rectangular bone extending from naris to orbit and bearing the lachrymal duct or ducts. In most long-snouted temnospondyls it withdraws from contact with the naris and orbit and is a rhomboidal bone bordered by nasal, maxillary, prefrontal, and jugal. In trematopids however, the enlarged naris, combined with the retention of the lachrymal position on the orbit margin, results in the lachrymal being preserved as a triangular plate of sculptured bone bordering the orbit anterolaterally. This is well shown by the trematopid *Actiobates*, also from Garnett (text-fig. 2A). A ventral process of bone extends anteriorly from the main body of the lachrymal along the floor of

the nasal chamber bordering the maxillary (text-fig. 2A) and this corresponds to the slender process which Eaton and Stewart interpreted as a form of tabular horn. The resultant configuration of a trematopid lachrymal is matched by the bone in KUVP 10295 (text-figs. 2B and 3) and this provides compelling evidence that the bone is a lachrymal and that the specimen is a trematopid temnospondyl.

The left postfrontal is present as an isolated element overlapping the left pterygoid (text-fig. 3). It is anteriorly pointed and posteriorly rectangular with a small posterior lappet which would have extended under the supratemporal. This shape of bone and the position of the lappet identify it as a postfrontal (Boy 1972 Abb. 4k depicts a very similar postfrontal in *Micromelerpeton*). It has temnospondyl-type irregular pitted sculpture and the absence of dermo-sensory pits or canals indicates that it derives from a terrestrial temnospondyl. In these features it is consistent with attribution to the families Eryopidae, Trematopidae, or Dissorophidae. The anterior extension terminating in a point rather than a sutural contact indicates that there was no prefrontal-postfrontal common suture but that both bones terminated as points over the orbit, and that the frontals entered the orbit margin. This derived character occurs in advanced dissorophids (not *Amphibamus*) and in trematopids, but not in eryopids where there is consistently a prefrontal-postfrontal contact. No bone of this precise shape was figured by Eaton and Stewart but it may be the 'postorbital' of their description.

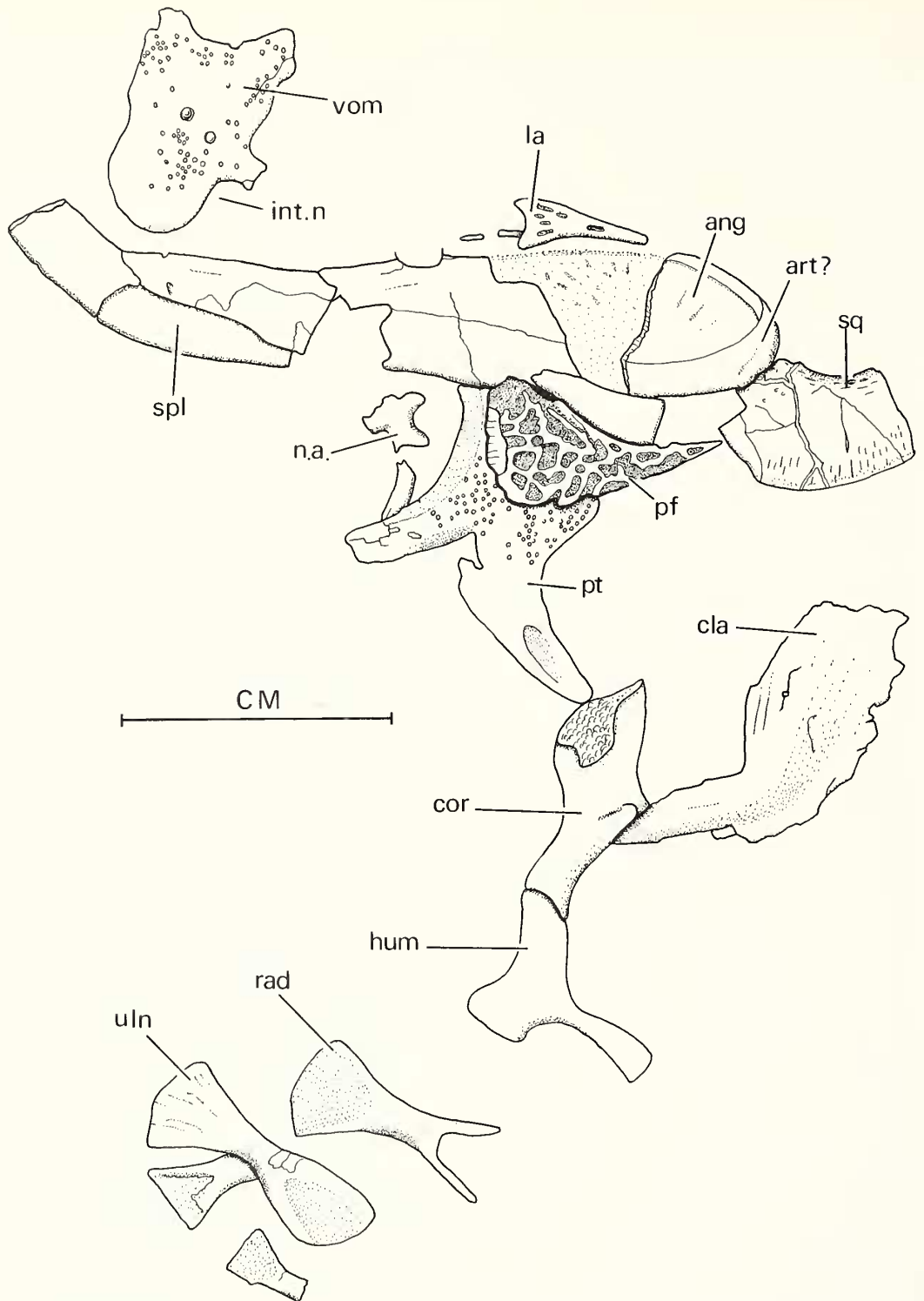
The right squamosal (text-fig. 3) was figured by Eaton and Stewart (1960, fig. 3a, b) as the left squamosal. It is a large rectangular bone, shallowly concave along one edge, which is the border of the tympanic notch, rather than the (unprecedented) orbit margin as suggested by Eaton and Stewart. The unsculptured ventral surface is exposed and on it, next to the otic margin, is a branched crack, the raised edges of which appear to have been figured as flange-like structures by Eaton and Stewart. Such flanges are not certainly present unless cracks have formed along the edges of them so that the structures which appear as raised edges are, in fact, low flanges. Flanges on the ventral surface of the squamosal have been reported in several Palaeozoic temnospondyls including *Edops* (Romer and Witter 1942), *Dendroperpeton* (Watson 1956, fig. 29 as *Platystegos*), *Tersomius* (Carroll 1964, fig. 4), and an unnamed trematopid from Fort Sill (Bolt 1974b, fig. 3). The squamosal only indicates the presence of a large otic notch.

The right vomer (text-fig. 3) is a large irregularly shaped flat plate of bone bearing a covering of tiny denticles and what appear to be the bases of two palatal fangs on the exposed ventral surface. A shallow concavity along one edge may be interpreted as the border of the internal naris. A slightly larger concavity on one of the shorter edges is probably the anterior border of the left interpterygoid vacuity. Such a large, relatively wide, vomer bearing a fang-pair and bordering a large interpterygoid vacuity is only consistent with belonging to a temnospondyl. Other early tetrapods either have narrow vomers, fangless vomers, or no interpterygoid vacuities.

The left pterygoid (text-fig. 3) is also denticle covered on the exposed ventral face and is of the characteristic triradiate form associated with the presence of large interpterygoid vacuities. The quadrate and basipterygoid rami are clearly visible and the palatine ramus is partly obscured by the superimposed postfrontal. There is also a distinct denticle-bearing posterodistal flange. The combination of such a flange with large interpterygoid vacuities identifies the specimen as a dissorophoid, either belonging to the Dissorophidae or the Trematopidae.

The above described elements are the only ones which could be identified as cranial ossifications. I could not recognize the premaxillary, maxillary, parietal, supratemporal, or any of the occipital and braincase ossifications identified by Eaton and Stewart. It would, of course, be futile to attempt a reconstruction of the skull based on the five elements recognized in this work, but they include most of the bones used in Eaton and Stewart's palatal reconstruction and some of the significant components of their skull roof reconstruction.

Mandible. The right mandible (text-fig. 3) is crushed and lightly twisted, being visible in dorsolateral aspect at the back and ventrolateral aspect at the front. It bears temnospondyl-type sculpturing on one large posterior element, partly visible as impression, which appears to me to be the angular rather than the surangular as suggested by Eaton and Stewart. Parts of the mandible may be identified as the



TEXT-FIG. 3. Indeterminate trematopid previously referred to *Hesperoherpeton garnettense* by Eaton and Stewart 1960. KUVP 10295, part of one face of the specimen showing disarticulated cranial and anterior appendicular elements. Abbreviations: ang—angular, art?—articular?, cla—clavicle, cor—coracoid, hum—humerus, int.n.—margin of internal naris, la—lachrymal, n.a.—neural arch, pf—postfrontal, pt—pterygoid, rad—radius, spl—splenial, sq—squamosal, uln—ulna, vom—vomere.

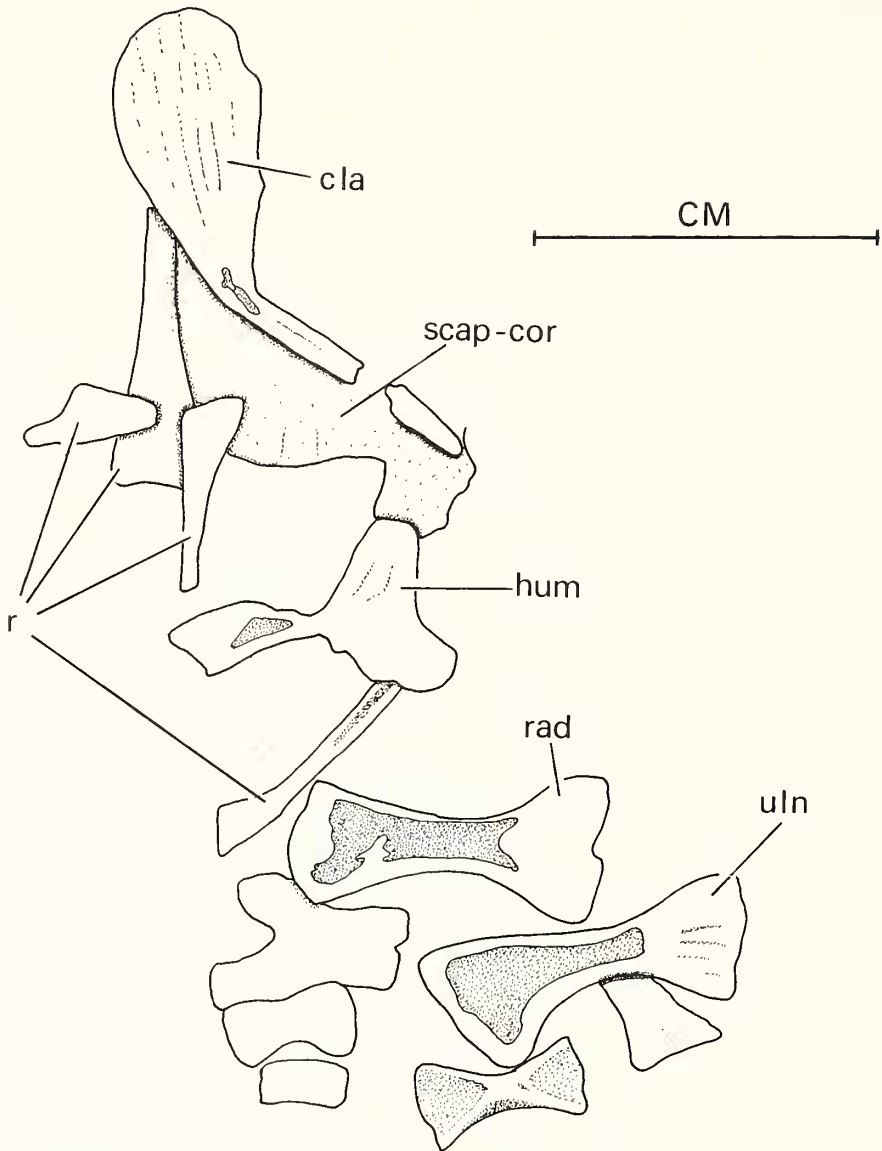
splenic, dentary, and articular with varying degrees of confidence but the only general conclusion that may be drawn from the mandible is that it probably belonged to a temnospondyl.

Postcranial skeleton. There is little to add to Eaton and Stewart's description of the vertebrae. They comprise neural arches, some with slightly elongate neural spines, U-shaped intercentra and large paired pleurocentra. Some neural spines are distinctly lower than depicted by Eaton and Stewart, one is visible in text-fig. 3 between the mandible and the pterygoid. The vertebrae appear to correspond to the typical rhachitinous condition and are consistent with attribution to many Palaeozoic temnospondyl families. Some short straight anterior thoracic ribs are present (text-fig. 4). As Eaton and Stewart note, they are substantially expanded proximally, but this is a common feature of the thoracic ribs of small labyrinthodonts.

Preparation of the slab has permitted both aspects of the preserved anterior appendicular skeleton to be recognized (text-figs. 3 and 4). The clavicle, visible in both aspects, is narrow-bladed with a long stem. The outer face of the blade is lightly striated. The narrow blade resembles those of presumed terrestrial temnospondyls such as eryopids, trematopids, and dissorophids and also of microsaur and seymouriamorphs. Part of the scapulocoracoid is visible under the clavicle on one side (text-fig. 4). A couple of striations are visible suggesting that part of the exposed bone is the scapular blade and the rest is coracoid. On the other face of the specimen (text-fig. 3) the crushed coracoid is visible in ventral aspect and bears a prominent glenoid fossa. Comparison of text-fig. 3 with figure 11 of Eaton and Stewart shows that their 'humerus' is actually the base of the coracoid with a short humerus closely appressed to it. They interpreted the coracoid as the ridged proximal region of an 'unusually long humerus' and the glenoid surface was depicted as an unfinished cartilage ridge on the proximal end of the humerus (Eaton and Stewart 1960, fig. 11).

The genuine humerus is a short 'propellor-blade' shaped structure with broad ends set at 90° to each other, the proximal end being visible as a flat blade while the distal end is visible only in section (text-figs. 3 and 4). This shape and relative size of humerus characterizes many terrestrial temnospondyls such as *Eryops*, the trematopids, and some dissorophids. In apparently aquatic temnospondyls such as the trimerorhachoids the humerus blades are poorly ossified and less obviously rotated at 90° to one another. Other small temnospondyls such as *Amphibamus* and *Branchiosaurus* have longer, more slender humeri (Carroll 1964; Boy 1972; Milner 1982). The humerus of KUVP 10295 was probably incompletely ossified at the ends and may have been slightly longer. Eaton and Stewart interpreted the entire humerus as the distal portion of a long humerus bearing a slender hook-like ectepicondyle, a supposed relictual fish characteristic. The radius and ulna are close to the humerus and to each other although not in articulation (text-figs. 3 and 4). They are of typical temnospondyl type and I cannot see the pronounced distal expansion of the ulna which Eaton and Stewart figure as homologous to a postaxial process. Several isolated metacarpals and phalanges are present but are not in articulation and do not permit a reconstruction of the carpus or manus. The only unusually shaped manus bone depicted by Eaton and Stewart which does appear to be present is the forked bone which they describe as an ulnare with a posterior hook-like expansion. A bone of approximately this shape is present on one face of the specimen (text-fig. 4). In view of the otherwise orthodox nature of the appendicular skeleton, I suspect that this ossification is made up of two or three metacarpals or phalanges superimposed and crushed across each other. Apart from this I can see nothing in the skeleton of the fore-limb which would justify the unique reconstruction of Eaton and Stewart.

Systematic position. The visible determinate bones of KUVP 10295 are all consistent with attribution to the Temnospondyli. The type of dermal sculpturing on the postfrontal, the shape of the pterygoid and the vomer, and the structure of the vertebrae in particular support this attribution. The postfrontal, squamosal, clavicle, and humerus together specify a temnospondyl with no lateral-line pits around the interorbital region, an otic notch, a narrow clavicle, and a short, broad-ended humerus showing pronounced torsion. Such characteristics are consistent with the specimen being either an eryopid, a dissorophid, or a trematopid. The pterygoid with the posterodistal flange and the postfrontal coming to an anterior point identify it as either a dissorophid or a trematopid, while the lachrymal is most diagnostic, permitting the specimen to be identified as a trematopid. The only other



TEXT-FIG. 4. Indeterminate trematopid previously referred to *Hesperoherpeton garnettense* by Eaton and Stewart 1960. KUV 10295, part of reverse face of specimen showing disarticulated axial and anterior appendicular elements. Abbreviations as for text-fig. 3 plus: r—rib, scap-cor—scapulocoracoid.

determinate amphibian described from Garnett is the trematopid *Actiobates peabodyi* (Eaton 1973) and it is probable though not demonstrable that KUV 10295 is a poor specimen of *Actiobates*. As *Actiobates* has not been fully described or comparatively diagnosed against the Texas red-bed trematopids such as *Acheloma*, there is no basis for assigning KUV 10295 to any particular genus other than by locality and horizon so it is proposed that the specimen be considered as Trematopidae *incertae sedis*.

DISCUSSION

Systematic conclusions. Re-examination of the two specimens from Garnett confirms a view, which has been implicit in the tendency of most workers to ignore Eaton and Stewart's paper, that their interpretation was not justified by the material and that there is no foundation for either the Order Plesiosauria or the Family Hesperoherpetonidae. Their limb reconstruction is based on a misinterpretation of the crushed anterior appendicular elements and their skull reconstructions are a frankly imaginative assembly of a series of isolated elements which can be interpreted in a far more justifiable manner by comparison with contemporaneous forms. As noted in the introduction, the nature of this specimen was immediately evident to most workers on Palaeozoic tetrapods and Eaton and Stewart's publication has been widely ignored. However because it was ignored rather than explicitly criticized, *Hesperoherpeton* found its way into several general discussions on the origin and early evolution of tetrapods, by authors who assumed that the absence of refutation meant that the work was accepted. It is, perhaps, a reminder of the value of published critical discussion.

Amphibians in the Garnett tetrapod fauna. The Garnett assemblage is unique among Carboniferous tetrapod assemblages in that it is largely composed of early amniotes, namely pelycosaurids and diapsids. Some of these have been redescribed or newly described in recent years and the known amniote fauna currently comprises the diapsid *Petrolacosaurus* (Reisz 1977, 1981) and four pelycosaurids, namely the sphenacodont *Haptodus* (Currie 1977, 1979), the enigmatic long-spined *Xyrospondylus* and undescribed material of *Edaphosaurus*, and a *Clepsydraps*-like ophiacodont (Reisz *et al.* 1982). The type specimen of the trematopid *Actiobates* (Eaton 1973) and the two specimens redescribed in this paper, are the only described amphibians from Garnett. Reisz *et al.* (1982) reported a further four amphibian specimens recently collected and yet to be described, while Peabody (1958, p. 571) reported an earlier discovery of a series of nectridean vertebrae which were subsequently lost before they could be described. Thus there may be other amphibians in the Garnett assemblage, but at present, all the described material is either trematopid temnospondyl or consistent with attribution to that family.

Reisz *et al.* (1982) discussed the lithology of the productive horizons at Garnett and concluded that it represents a terrestrial environment subject to progressive incursions by brackish water, implying an estuarine mud-flat regime. It is interesting then, that the only determinate amphibians described to date are trematopids, the peculiar naris of which has been interpreted as modified to incorporate a chamber for an enlarged gland, possibly a salt gland (Bolt 1974a). Possession of a salt gland permits tetrapods to be more tolerant of both xeric and saline environments and it is possible that trematopids had such glands and were unusual among temnospondyls in their tolerance of brackish conditions.

Acknowledgements. I should like to thank Dr Larry Martin and Dr Hans-Peter Schultze of the University of Kansas for their hospitality and for permission to examine this material. My research travel was funded by the University of London Central Research Fund.

REFERENCES

- ALEXANDER, R. MCN. 1975. *The Chordates*, 480 pp. Cambridge University Press, London.
- BOLT, J. R. 1974a. Osteology, function and evolution of the trematopsid (Amphibia: Labyrinthodontia) nasal region. *Fieldiana: Geol.* **33**, 11–30.
- 1974b. A trematopsid skull from the Lower Permian, and analysis of some characters of the dissorophoid (Amphibia: Labyrinthodontia) otic notch. *Ibid.* **30**, 67–79.
- BOY, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). *Abh. hess. Landesamt. Bodenforsch.* **65**, 1–137.
- 1981. Zur Anwendung der Hennigschen Methode in der Wirbeltierpaläontologie. *Paläont. Z.* **55**, 87–107.
- CARROLL, R. L. 1964. Early evolution of the dissorophid amphibians. *Bull. Mus. comp. Zool. Harv.* **131**, 163–250.
- and WINER, L. 1977. Privately circulated appendix to CARROLL, R. L. Patterns of amphibian evolution: an extended example of the incompleteness of the fossil record. Chapter 13 in HALLAM, A. (ed.). *Patterns of Evolution*. Elsevier, Amsterdam.

- CHASE, J. N. 1965. *Neldasaurus wrightae*, a new rhachitinous labyrinthodont from the Texas Lower Permian. *Bull. Mus. comp. Zool. Harv.* **133**, 153–225.
- CURRIE, P. J. 1977. A new haptodontine sphecnacodont (Reptilia: Pelycosauria) from the Upper Pennsylvanian of North America. *J. Paleont.* **51**, 927–942.
- 1979. The osteology of haptodontine sphecnacodonts (Reptilia: Pelycosauria). *Palaeontographica* Abt. A. **163**, 130–168.
- DALY, E. 1973. A Lower Permian vertebrate fauna from southern Oklahoma. *J. Paleont.* **47**, 562–589.
- DEMAR, R. E. 1966. *Longiscitula houghae*, a new genus of dissorophid amphibian from the Permian of Texas. *Fieldiana: Geol.* **16**, 45–53.
- 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus* and the adaptations and phylogeny of the family Dissorophidae. *J. Paleont.* **42**, 1210–1242.
- EATON, T. H. JR. 1951. Origin of tetrapod limbs. *Amer. Midl. Nat.* **46**, 245–251.
- 1960. The aquatic origin of tetrapods. *Trans. Kans. Acad. Sci.* **63**, 115–120.
- 1973. A Pennsylvanian dissorophid amphibian from Kansas. *Occas. Pap. Mus. nat. Hist. Univ. Kans.* **14**, 1–8.
- and STEWART, P. L. 1960. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. *Univ. Kans. Publs Mus. nat. Hist.* **12**, 217–240.
- HOLMES, R. 1980. *Proterogyrinus scheelei* and the early evolution of the labyrinthodont pectoral limb, 351–376. In PANCHEN, A. L. (ed.). *The terrestrial environment and the origin of land vertebrates*, 633 pp. Systematics Assn Spec. Vol. No. 15. Academic Press, London.
- KUHN, O. 1972. Seymourida, 20–69. In CARROLL, R. L., KUHN, O. and TATARINOV, L. P. Teil 5B Batrachosauria (Anthracosauria), Gephyrostegida–Chroniosuchida. *Handbuch der Paläoherpetologie*. Fischer, Stuttgart.
- MILNER, A. R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology*, **25**, 635–664.
- MOULTON, J. M. 1974. A description of the vertebral column of *Eryops* based on the notes and drawings of A. S. Romer. *Breviora*, No. 428, 1–44.
- OLSON, E. C. 1941. The family Trematopsidae. *J. Geol.* **49**, 149–176.
- 1971. *Vertebrate Paleozoology*, 839 pp. Wiley Interscience, New York.
- PEABODY, F. E. 1958. An embolomeroous amphibian in the Garnett fauna (Pennsylvanian) of Kansas. *J. Paleont.* **32**, 571–573.
- PORTER, K. R. 1972. *Herpetology*, 524 pp. Saunders, Philadelphia.
- REISZ, R. R. 1977. *Petrolacosaurus kansensis* Lane, the oldest known diapsid reptile. *Science*, **196**, 1091–1093.
- 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Spec. Publ. Mus. nat. Hist. Univ. Kans.* **7**, 1–74.
- HEATON, M. J. and PYNN, B. R. 1982. Vertebrate fauna of late Pennsylvanian Rock Lake Shale near Garnett, Kansas: Pelycosauria. *J. Paleont.* **56**, 741–750.
- ROMER, A. S. 1966. *Vertebrate Paleontology* (3rd edn), 468 pp. Chicago University Press, Chicago.
- 1968. *Notes and Comments on Vertebrate Paleontology*, 304 pp. Chicago University Press, Chicago.
- and WITTER, R. V. 1942. *Edops*, a primitive rhachitinous amphibian from the Texas red beds. *J. Geol.* **50**, 925–960.
- ROSEN, D. E., FOREY, P. L., GARDINER, B. G. and PATTERSON, C. 1981. Lungfishes, tetrapods, paleontology and plesiomorphy. *Bull. Am. Mus. nat. Hist.* **167**, 159–267.
- SCHMALHAUSEN, I. I. 1968. *The Origin of Terrestrial Vertebrates*, 314 pp. Academic Press, New York and London.
- THOMSON, K. S. and BOSSY, K. H. 1970. Adaptive trends and relationships in early Amphibia. *Forma et Functio*, **3**, 7–31.
- TVERDOCHLEBOVA, G. I. 1972. A new batrachosaurian genus from the Upper Permian of southern Cisuralia. *Paleontol. J.* **6**, 84–90.
- VOROB'YEVA, E. I. 1974. On the formation of tetrapod characters in crossopterygians. *Ibid.* **8**, 219–224.
- WATSON, D. M. S. 1956. The brachyopid labyrinthodonts. *Bull. Br. Mus. nat. Hist. (Geol.)*, **2**, 315–392.

ANDREW R. MILNER
Department of Biology
Birkbeck College
London WC1E 7HX